

GENETIC STUDIES IN LYCOPERSICUM

I. THE HEREDITY OF FRUIT SHAPE IN THE GARDEN TOMATO

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INTRODUCTION

THIS paper presents field observations bearing upon the heredity of fruit shape in the common garden tomato, *Lycopersicum esculentum* Mill., together with a simple Mendelian hypothesis which explains the heredity of several fruit types, and an analysis of data recorded by previous investigators in the light of the hypothesis suggested.

PREVIOUS MENDELIAN STUDIES IN THE GENUS LYCOPERSICUM

Previous Mendelian studies in the genus *Lycopersicum* account for the heredity of nine characters on a monohybrid basis. In a list (See Table I) revised from the data of Halsted (1905) and Price and Drinkard (1908), Jones (1917) gives eleven such characters involving various parts of the plant, and including two fruit shape characters, but with certain reservations as to the validity of the assumption that fruit shape is determined in any case by a single pair of factors. The original data of Price and Drinkard are meager and are not considered by the authors themselves as conclusive proof of the monohybrid nature of the types recorded. Groth (1912, 1915) and Crane (1915) find difficulty in classifying the various shapes which segregate in F_2 progenies of crosses between varieties differing in fruit shape, and assume that several factors are involved. Groth (1915),

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in fact, arrives at no particular conclusions as to the interpretation of his own data, except that Mendelism is inadequate to account for the behavior of thousands of plants in his gardens, and that a stimulus imparted to the soma by the germ plasm must be invoked to explain the "Golden Mean" in F_1 and the chaos in F_2 . Emerson (1917) has shown that the phenomena observed by Groth may be explained by the theory of multiple factors.

Preliminary observations upon the character of fruit produced in 1919 by homozygous strains of ten garden varieties indicated (1) that each variety produces a fruit of definite shape and size; (2) that the fruits of some varieties are deep, those of other varieties shallow; (3) that the fruits of certain varieties are fasciated, i.e., they represent a fusion of two or more ovaries, those of other varieties non-fasciated; and (4) that each fruit shape represents a separate combination of the unit characters, deep and shallow, fasciated and non-fasciated. These observations have since been confirmed by field records and quantitative data upon the progeny of all parent strains and many crosses.

Deep fruits are easily distinguished from shallow fruits without resorting to the caliper. Fasciated fruits are distinguished from non-fasciated fruits either by their shape or, more accurately, by the nature of the flower scar. Appropriate crosses have been made and fruit shape records of more than seven thousand plants are here presented, which seem to indicate that deep and shallow, fasciated and non-fasciated hitherto unrecognized as unit characters, are indeed such. Furthermore, it has been possible to identify the factors which determine them. Deep fruits are produced by the complementary factors *A* and *B*, non-fasciated fruits by the complementary factors *F* and *E*.

If this hypothesis be accepted, it is no longer possible to assume, with Price and Drinkard, that any fruit shape (e.g., roundish-conic) is a unit character. The data here presented are not in accord with any multiple factor hypothesis, since there is always distinct segregation in the F_2 .

MATERIAL AND METHODS

ORIGIN AND DESCRIPTION OF THE VARIETIES INVESTIGATED

Ten strains of tomato, representative of all fruit shapes found among garden varieties, were selected and crossed. Progeny of the parent strains and the F_1 and F_2 generations from crosses were grown in 1920 and 1921. In Table II are shown the pedigrees of all parents and crosses.

All of the strains were obtained from the Jerome B. Rice Seed Co. through the kindness of Mr. Wilber Brotherton, manager of the Detroit branch, to whom the writer is greatly indebted for coöperation in many ways. With the exception of Bolgiano and Discovery, these strains have been under observation for years by Mr. George Starr, plant breeder for the Company, at the Grass Lake Stock Seed Farm. To him the writer is under obligation for supplying strains of known history and great uniformity. These with the exception of Discovery have proved homozygous for all characters. Although Mr. Starr does not practice artificial pollination, his method of selection involves sufficient isolation to preclude the possibility of the accidental introduction of pollen foreign to the variety. Artificial self-pollination of each strain, in some cases to the fourth generation, has failed to reveal a single segregating character in all but the single variety mentioned.

A brief detailed description of each variety follows. The classification is in accord with the depth-fasciation hypothesis and the genotypic formula is supplied here for later reference.

*I. Varieties with deep, non-fasciated fruits*1. Early Detroit, *AABBFEE*

A homozygous strain of this variety has been under observation for four generations. The fruit is pink, deep (Globe type) and always non-fasciated. The name of the variety is misleading. The plants produce fruit very late in the season.

2. Discovery. It is impossible to assign a formula to this

variety. The plant used in the original cross was of the formula *AaBbFfEe*.

Of all varieties, Discovery is the most irregular. Except for stature, leaf margin and fruit color, the strain was heterozygous when received. The behavior in heredity of the variety indicates that it may have resulted from a recent cross between a Globe type and a member of the Earliana, Bolgiano, June Pink group. Seed was sent to Mr. Brotherton by Lottentot and Huber, seedsmen, and large cultures have been grown at Ann Arbor and at Grass Lake with the same result, a splitting into two or more types in each generation. The typical Discovery fruit is deep, non-fasciated.

II. Varieties with deep, fasciated fruits

1. Ponderosa, AABbffee

Ponderosa is a well known late variety with deep, much fasciated, pink fruit. The plants are exceptionally large, a characteristic which is usually associated with late fruit production.

2. John Baer, AABBFfee

John Baer is especially prolific and early. The fruits are red, deep, usually fasciated, but never of the tremendous size of those in Ponderosa.

3. Imperial, AABBFfee

Imperial is a very late variety, erect in habit, very vigorous in growth, producing deep, pink fruits, similar to those of John Baer, but of better quality.

III. Varieties with shallow, non-fasciated fruits

1. Dwarf Stone, aabbFFEE

A very late variety, Dwarf Stone produces rather small red fruits on erect, vigorous plants.

IV. Varieties with shallow, fasciated fruits

1. Bolgiano, aabbffEE

A potato-leaf red-fruited variety, lauded by its discoverer,

Bolgiano, for its extreme earliness, was sent to Mr. Brotherton in 1919 with permission to employ it for breeding purposes. Several plants were furnished to the writer in the spring of 1920. It proved to be as early as the Rice Company's best strain, Earliana. As in all early varieties, the habit of the plant is low and sprawling, the leaves are small and the fruits much smaller and more inclined to sun-cracking than those of the later, more vigorous types. Each plant produces a preponderance of shallow, non-fasciated fruits, but always a number of shallow, fasciated fruits.

2. Earliana, *aabbffEE*

A homozygous strain, selected for the shape, texture and color of fruit as well as for earliness, Earliana is very similar to Bolgiano, differing only in that the leaves have serrate margins.

3. June Pink, *aaBBffee*

June Pink owes its name to the combination of earliness and pink (i.e., red endocarp and colorless epicarp) fruit color. The habit is low and sprawling. That there is a certain relationship between this variety and the large-fruited variety Ponderosa is evidenced by two facts, (1) the leaves of both varieties are crinkly at the edges and (2) a plant producing fruit identical with that of Ponderosa appeared in the cultures in the summer of 1921 as a mutation. The fruits are shallow, but much fasciated.

4. Dwarf Champion, *aabbffee*

The strain under observation is extremely uniform. Unlike the other varieties it produces ripe fruit in the middle of the season. The fruits are pink, very shallow and fasciated in about the same percentage as in Bolgiano. The plants are of dwarf stature, grow rapidly, and soon lop over to the ground.

METHOD OF POLLINATION

The methods of pollinating the flowers and of growing the cultures may be outlined briefly. The tomato flower, normally self-fertilized, is easily emasculated and pollinated. The young

peduncle is very fragile, however, and it has been found convenient to depart from the usual custom of protecting the pollinated flower with paper bags and to resort to the use of two-inch squares of heavy tissue paper. The paper is formed into a cap, securely wired over the pollinated flower, and allowed to remain until the style has fallen, usually about four days. Emasculation and pollination are accomplished at the same time. A young flower is selected from the pollen parent, the pollen extracted and applied with a pollinating knife immediately after the flower of the staminate parent has been emasculated.

METHOD OF HARVESTING SEED

Seed are harvested from the ripe fruits as follows. After the desired measurements are made, the fruit is cut transversely through the center and a record taken of the number of locules. The pulp is squeezed out into water in a battery jar and the mass mixed thoroughly. A bit of inoculum from a jar containing fruit pulp which has been allowed to ferment in water for several days is added. After a day the fermented mass is washed with a stream of water in a piece of cloth suspended over a cylinder of wire screen and the seed spread out on paper towels to dry.

WINTER AND SUMMER CULTURES

Since it is desirable to have the cultures of all generations of a series in the gardens at the same time, winter cultures in the greenhouse are grown merely to produce seed. Crosses are usually made in the garden. Progeny from the parents and a few F_1 plants are grown in the greenhouse for self-pollination. In the spring the seed from the parents, the seed remaining from the original crosses and the seed obtained from the F_1 plants, are planted for the field cultures. In this way it has been possible to study an extra generation on a large scale each year and to base all conclusions on plants grown in the garden.

In order to grow plants in the winter in the latitude of Ann Arbor with the assurance of ripe seed in time for the spring planting, it is necessary to resort to extreme forcing methods.

The plants are grown in a mixture of one part sand and two parts loam to prevent an excess of vegetative growth. Each plant is watched closely for the appearance of the first flower cluster, and the necessary pollinations are made at once. The energy of the plant is now directed to the rapid development of ripe fruit by the frequent removal of new clusters and vegetative growth which may appear.

Cultures in the greenhouse are limited to about four plants each. Field cultures are much larger. More than seven thousand plants were grown in the gardens in 1921. The ideal series of cultures for each cross consists of (1) each parent, A and B, one hundred plants, (2) F_1 pedigrees to include the reciprocal crosses, $A \times B$ and $B \times A$, each fifty plants, (3) F_2 pedigrees, $A \times B$, self-pollinated and $B \times A$, self-pollinated, each seventy-five plants and (4) back-crosses, each one hundred and twenty-five plants. Such a series of cultures has not always been grown for each of the crosses, in some cases because of lack of time to make thorough observations. More important series are always given precedence.

ALTERNATIVE METHODS OF INVESTIGATION

Two avenues of approach are open to an investigator of the heredity of size and shape in the higher plants. If the material be favorable, a direct classification of the parents, F_1 and F_2 segregates, may be made; if unfavorable for such a classification, large series of measurements are necessary. In the former case the validity of the interpretation of the results is dependent upon the magnitude of the observable differences between the classes. In the latter case, since there are no distinct classes, the data must be analyzed biometrically, and the value of the interpretation, speculative in great measure, depends upon the individual skill of the investigator in the treatment of the observed adherence to or departure from the Gaussian distribution, as an index to the behavior of the unit characters.

Ample proof of the truth of these generalities is presented in previous papers upon the heredity of size and shape in the

tomato. Price and Drinkard (1908) have arrived at certain conclusions as to fruit shape by the method of direct classification. Groth's statistical methods have led him to conclusions which have brought severe criticism (Emerson, 1917). The earlier writers observe the types of fruit, and conclude that there is a definite Mendelian interpretation to be placed upon the observed segregations; the later writer becomes involved in a labyrinth of frequency distributions derived from individual fruit measurements, and comes to the conclusion that none of the neoteric developments of Mendelism are of avail in the explanation of the observed phenomena.

In the present investigation both methods have been employed. Many plants have been classified as to the depth and fasciation of their fruits by direct observation. In certain cultures the weight and size of the fruits have been determined. These quantitative data confirm the accuracy of the former method in every case. Only such constants derived from them as are needed for the purpose of definition will be presented here. It is proposed to publish these data in full in papers devoted entirely to discussions of the quantitative measurement of fruit size in relation to the depth-fasciation hypothesis, to hybrid vigor and allied phenomena.

THE RESULTS OF HYBRID SEGREGATION

Ratios among the F_2 segregates from crosses between the several varieties do not conform to a monohybrid hypothesis. Attempts to explain the observed ratios on a dihybrid or polyhybrid basis, involving dominance, have also failed. If the following pairs of complementary factors are assumed to be operative in the determination of the types of fruit observed in F_1 and in the F_2 , it is possible to explain every phenomenon which has thus far been observed in the crosses.

FACTORS FOR DEPTH AND FASCIATION

A, a factor which alone produces shallow fruits, but which in the presence of *B* produces deep fruits.

a, the normal allelomorph of *A*; produces fruits slightly more shallow than *A*.

B, a factor which alone produces shallow fruits, but in the presence of *A*, deep fruits.

b, the normal allelomorph of *B*; behaves as *a*.

F, a factor which alone produces fasciated fruits, but in the presence of *E*, non-fasciated fruits.

f, the normal allelomorph of *F*; alone produces much fasciated fruits.

E, a factor which alone produces fasciated fruits, but in the presence of *F*, non-fasciated fruits.

e, the normal allelomorph of *E*; behaves as *f*.

Combinations of the factors suggested determine the shape of the fruit as follows:

GROUP	GENOTYPE	PHENOTYPE	SHAPE
1.	<i>ABFE</i>	Deep, non-fasciated	Deep-round
2.	<i>ABFe</i> , <i>ABfE</i> , or <i>ABfe</i>	Deep, fasciated	Deep-round or Deep-oval
3.	<i>AbFE</i> , <i>aBFE</i> , or <i>abFE</i>	Shallow, non-fasciated	Shallow-round
4.	<i>AbFe</i> , <i>abFe</i> , <i>abfe</i> , <i>AbfE</i> , <i>abfE</i> , <i>aBfE</i> , <i>aBFe</i>	Shallow, fasciated	Shallow-round or Shallow-oval

As a result of the behavior of each of the ten varieties in crosses, it has been possible to assign to each the complete genotypic formula given with the variety descriptions.

The factors for non-fasciation behave in a manner which has not yet been suggested. *F* in the presence of *E* always produces a non-fasciated fruit. Either of these factors, however, in the homozygous condition (*FF* or *EE*) inhibits fasciation to a slight degree. For example, in *Bolgiano*, *Imperial* and *John Baer* the presence of *EE*, *FF* and *FF* respectively inhibits the complete fasciation found in *June Pink* and *Ponderosa*. The factors *A* and *B* may behave in a similar manner.

In Table III are given all of the possible combinations of the four pairs of factors *A*, *a*; *B*, *b*; *F*, *f*; and *E*, *e*, with the progeny to be expected from self-fertilized plants of each genotypic constitution. All of the varieties fall into the first four groups of Table III and breed true for their individual types ex-

cept the variety Discovery. This variety gives progeny which may fall into any of the sixteen groups. An individual plant of this variety which was used in certain crosses was of the formula *AaBbFfEe*. Upon self-pollination it gave a close approach to the ratio 81 deep, non-fasciated: 112 shallow, non-fasciated and fasciated: 63 deep, fasciated.

The actual ratio is 90.1:97.3:68.5.

The deviation is 9.1:14.6: 5.5.

The probable error is 9.5: 9.0: 8.8.

The Dev./ P. E. is 1.0: 1.6: 0.6.

By the χ^2 method, $\chi^2 = .951$ and $P = .799331$.

CLASSIFICATION OF CROSSES

The crosses which were used to test the foregoing hypothesis fall into the following groups, arranged in accordance with the order of Table III.

1. CROSSES in which the F_1 falls into one of the first four groups of Table III and in which there is no segregation for fruit shape in F_2 (Crosses I–VI).

- I. Bolgiano $\times$ June Pink
- II. Bolgiano $\times$ Earliana
- III. Earliana $\times$ June Pink
- IV. Dwarf Champion $\times$ Bolgiano
- V. Dwarf Champion $\times$ June Pink
- VI. Ponderosa $\times$ John Baer

2. CROSSES in which the F_1 falls into Group 5 of Table III, namely, those in which the F_2 segregation is 3 deep, fasciated: 1 shallow, fasciated (Cross VII).

- VII. June Pink $\times$ Ponderosa

3. CROSSES in which the F_1 falls into Group 8 of Table III, namely, those in which the F_2 segregation is 3 shallow, non-fasciated: 1 shallow, fasciated (Cross VIII).

- VIII. Bolgiano $\times$ Dwarf Stone

4. CROSSES in which the F_1 falls into Group 9 of Table III,

namely, those in which the F_2 segregation is 9 deep, non-fasciated: 7 deep, fasciated (Cross IX).

IX. Ponderosa $\times$ Early Detroit

5. CROSSES in which the F_1 falls into Group 10 of Table III, namely, those in which the F_2 segregation is 9 deep, fasciated: 7 shallow, fasciated (Cross X).

X. Bolgiano $\times$ Ponderosa

6. CROSSES in which the F_1 falls into Group 14 of Table III, namely, those in which the F_2 segregation is 27 deep, non-fasciated: 21 deep, fasciated: 9 shallow, non-fasciated: 7 shallow, fasciated (Cross XI).

XI. Early Detroit $\times$ June Pink

7. CROSSES in which the F_1 falls into Group 15 of Table III, namely, those in which the F_2 segregation is 27 deep, non-fasciated: 21 shallow, non-fasciated: 9 deep, fasciated: 7 shallow, fasciated (Crosses XII–XIII).

XII. Bolgiano $\times$ Early Detroit

XIII. John Baer $\times$ Dwarf Stone

8. CROSSES in which the F_1 falls into Group 16 of Table III, namely, those in which the F_2 segregation is 81 deep, non-fasciated: 63 shallow, non-fasciated: 63 deep, fasciated: 49 shallow, fasciated (Crosses XIV–XVII).

XIV. Early Detroit $\times$ Dwarf Champion

XV. Bolgiano $\times$ John Baer

XVI. Ponderosa $\times$ Dwarf Stone

XVII. Imperial $\times$ Bolgiano

9. CROSSES in which the F_1 falls into several groups because of the heterozygosis of one of the parents and in which the segregation in the F_2 depends upon the genotypic constitution of the self-pollinated F_1 individual (Crosses XVIII–XXI).

XVIII. Discovery $\times$ Ponderosa

XIX. Discovery $\times$ Bolgiano

XX. Discovery $\times$ Earliana

XXI. Discovery $\times$ June Pink

The F_2 ratios from all of these crosses are presented in Table V. The genotypic formulae of many varieties have been determined by several crosses. A record of all genotypes investigated is presented in Table IV. It is evident from the situation which obtains in the first group above, that the genotypic constitution of Bolgiano, June Pink, Earliana and Dwarf Champion could not be discovered by any series of crosses within the group. Crosses between these varieties and the six remaining varieties under observation have brought forth the interesting segregation phenomena observed in the last nine groups.

TESTS FOR GOODNESS OF FIT

Before each cross is discussed in detail, a word must be said as to the tests applied for goodness of fit of the Mendelian ratios of Table V. In all cases the probable errors have been calculated by the orthodox modification of the $\sqrt{npq}$ formula for the standard deviation (σ). In this method the

$$P E = \pm 0.67449 \sqrt{\frac{N(K-N)}{n}}$$

where P E is the probable error, N a particular term of a Mendelian ratio, K the sum of all the terms of such a ratio, and n the total number of individuals involved in the classification. Such a procedure involves the assumption that the standard deviation of a ratio is equal to $\pm \sqrt{N(K-N)}$, a sufficiently valid assumption in any case, provided the number of observed individuals is large, certainly of value in the consideration of such ratios as 1:1 and 9:7, even though the number of individuals be comparatively small. Wherever possible, i.e., in such ratios as 48:9:7 and 144:63:49, in which more than two terms are involved, the probability (P) of the occurrence of such a ratio as a result of random sampling has been calculated by the χ^2 method of Pearson in which

$$\chi^2 = \sum \left(\frac{(m - m^1)^2}{m} \right),$$

where the expression $\sum \left(\frac{(m - m^1)^2}{m} \right)$ signifies the sum of all such terms as the square of the difference between the observed fre-

quency and the theoretical frequency, divided by the theoretical frequency. The probability integral (P) is calculated from Elderton's *Tables for Goodness of Fit*. (Pearson, 1914.) Constants derived by this method are given in the text in the discussion of the crosses.

DISCUSSION OF CROSSES

1. CROSSES in which the F_1 falls into Groups 1-4 of Table III and no segregation takes place in the F_2 generation.

I. Bolgiano, $aabbffEE \times$ June Pink, $aaBBffee$

$F_1 = aaBbffEe$

The parents as well as the F_1 and F_2 generations in this cross produce shallow fasciated fruits. June Pink has deeper fruits than Bolgiano because of the presence of the factor B in the homozygous condition; more completely fasciated, consequently heavier fruits than Bolgiano because of the absence of the inhibiting factors EE . The F_1 fruits are intermediate in both depth and fasciation. These differences have been measured and found significant. It is impossible by direct observation to record the small differences in depth and fasciation brought about by the factors B and E alone. These must be treated in another paper devoted to the presentation of quantitative data.

II. Bolgiano, $aabbffEE \times$ Earliana, $aabbffEE$

F_1 and F_2 , $aabbffEE$

The genotypic formulae here given have been determined from other crosses. The varieties Bolgiano and Earliana bear identical types of fruit. No differences possible of record by direct observation have been found in the fruits of the parents, the F_1 or the F_2 in this cross.

More than three thousand fruits have been measured in this series in a separate investigation of hybrid vigor and these data will be presented elsewhere.

III. Earliana, $aabbffEE \times$ June Pink, $aaBBffee$

F_1 , $aaBbffEe$

Obviously this cross involves the same genetic possibilities as the cross Bolgiano $\times$ June Pink. The result is the same. No segregation occurred in the F_2 . The quantitative data are strictly comparable to those in the former cross.

IV. Dwarf Champion, *aabbffee* $\times$ Bolgiano, *aabbffEE*
 F_1 , *aabbffEe*

Forty-six plants of the F_1 and 151 plants of the F_2 were grown, mainly for the purpose of testing linkage between the potato-leaf and dwarf characters, a matter which will be discussed in another paper.

None of the fruits were measured. The parents, the F_1 and the F_2 , are all shallow and more or less fasciated.

V. Dwarf Champion, *aabbffee* $\times$ June Pink, *aaBBffee*
 F_1 , *aaBbffee*

The F_1 generation with 64 plants, the F_2 with 148 plants, the back-cross June Pink $\times$ (June Pink $\times$ Dwarf Champion) with 124 plants and the back-cross Dwarf Champion $\times$ (June Pink $\times$ Dwarf Champion) with 124 plants have all failed to produce any fruits not to be expected from the foregoing formulae. The fruits vary somewhat in size but are all fasciated and are all shallow. In the F_2 generation it was possible to make a rough classification into 106 bearing slightly deeper and 42 bearing slightly shallower fruits. The ratio is 2.9:1.1, a close correspondence to the 3:1 ratio expected from the segregation of *Bb* in the F_1 . No such classification was attempted in the back-crosses.

VI. Ponderosa, *AABBffee* $\times$ John Baer, *AABBFFee*
 F_1 , *AABBFFee*

Ponderosa is a deep-fruited variety in which every fruit is fasciated, generally to the extent of producing exceedingly large misshapen fruits. John Baer is also deep-fruited and the fruits are somewhat fasciated, but never to the degree observed in Ponderosa, a fact which is accounted for by the presence in John Baer of the *F* factor in the homozygous condition. Eight

plants of the F_1 produced fruits which were also deep, but intermediate between the parents in fasciation, as would be expected in the heterozygous (Ff) type.

In F_2 it should be possible to make a rough classification on the basis of fasciation alone. All plants bear fasciated fruits. The difference is one of degree, as would be expected by the presence in this generation of plants 25 per cent of which are homozygous for F , 50 per cent in the Ff condition and 25 per cent in the ff condition. It has not been possible to differentiate two of these classes. The ff class, however, is fairly distinct from the others and the field records show 24 such plants to 75 of the Ff and FF plants, a ratio of 0.97:3.03. The difference is 0.26 times the error and insignificant (See Table V).

In the back-cross $Ponderosa \times (June\ Pink \times Ponderosa)$, which should give by the same classification a ratio of 1:1 between the plants which bear more fasciated and those which bear less fasciated fruits, the ratio 61:49 or 1.11:0.89 was found. In this case the difference is 1.70 times the error and likewise insignificant (See Table V).

In the back-cross $John\ Baer \times (John\ Baer \times Ponderosa)$, all of the individuals ought to fall into the less fasciated class of the foregoing classification, as they were indeed found to do in a record of 186 plants.

It is rarely possible to observe the small differences recorded in this cross between offspring from plants of the formula Ff or Ee . As will be seen directly, the F_2 segregation is dependent mainly upon interaction of the factors F and E to prevent fasciation and of the factors A and B to produce deep fruits. It may be objected that, after all, the hypothesis suggested to account for the heredity of depth and fasciation is little more than a manipulation of a series of factors which have only a cumulative effect. That such an objection is not a valid one, and that, although the factors A , B , F and E may exhibit a cumulative effect to a certain degree, such an effect cannot account for the profound differences observed when the pairs A and B , F and E meet in a zygote, will be seen in the crosses about to be discussed.

2. CROSSES in which the F_1 falls into Group 5 of Table III, namely, those in which the F_2 segregation is 3 deep, fasciated: 1 shallow, fasciated (Cross VII).

VII. June Pink, *aaBBffee* $\times$ Ponderosa, *AABBffee*

F_1 , *AaBBffee*

The genotypic formulae in this series indicate that all of the individuals should bear fasciated fruits, and, since no *F* nor *E* factor is present, very much fasciated fruits. In all, 128 plants of the parent Ponderosa, 118 of June Pink, 95 of the F_1 , 132 of the F_2 , 129 of the back-crosses to Ponderosa, and 436 of the back-crosses to June Pink, a total of 1038 plants, has been grown. All of these plants have produced fasciated fruits. The reason for such an extensive series of cultures may be briefly outlined. In the opinion of the seedsmen June Pink and Ponderosa are closely allied varieties. The former is an early variety and produces smaller fruits, the latter a mid-season, sometimes considered a late variety, which produces the largest tomatoes known. Both varieties have crinkly leaves. A type similar to Ponderosa has appeared by mutation from June Pink. It would seem of particular interest to determine whether such a relationship could be assumed to bear upon the general shape and size of the fruits.

The first cross was made in 1919. The F_1 and F_2 cultures from this cross were grown in the 1920 garden. The series presented what appeared at first to be a case of blending inheritance. The cross was repeated and a second series including duplicates of the first series and in addition three F_3 cultures from the original cross were grown in the 1921 garden. Again the F_1 and F_2 cultures seemed to be so nearly alike that no attempt was made to classify the F_2 plants as to fruit shape and the fruits were recorded as intermediate. The importance of such a classification was not realized, in fact, until the present hypothesis had been worked out with other crosses and the formulae of June Pink and Ponderosa established.

A second perusal of the 1920 data brings to light several interesting facts which were not before considered important.

Twenty-six plants in the F_2 of that year are recorded as Ponderosa, six plants as June Pink, a ratio of 3.25:0.75. (See Table V). A 3:1 ratio is to be expected, since the F_2 falls into four equal classes, three of which have the factors *AABB* or *AaBB*, and one the factors *aaBB*. The three former classes are deep, corresponding to Ponderosa, the latter class shallow, as in June Pink.

Three F_3 cultures were grown in 1921 from the foregoing F_2 , one from a plant recorded as June Pink (i.e., shallow, fasciated), and two from plants recorded as Ponderosa (i.e., deep, fasciated). The former culture produced fruits which were recorded as intermediate. It is likely that close attention to this culture would have revealed a 3:1 segregation. The last two cultures were undoubtedly from the plants of the formula *AABBffee*, since they contained only large plants which produced typical, deep, fasciated Ponderosa fruits.

The back-crosses, June Pink $\times$ (June Pink $\times$ Ponderosa) and (June Pink $\times$ Ponderosa) $\times$ June Pink, grown in 1920, showed a segregation into 142 plants with fruits recorded as Ponderosa or "deep June Pink" to 123 plants with fruits recorded as "true June Pink," a ratio of 1.07:0.93. (See Table V). From the hypothesis the segregation should be in the ratio 1 deep, fasciated: 1 shallow, fasciated. It is possible that some of the June Pink plants may have been recorded as Ponderosa, thus accounting for the excess of the latter plants in the ratio. A classification with regard to depth in fasciated fruits is sometimes difficult to make without actually measuring the fruits.

The back-crosses, Ponderosa $\times$ (June Pink $\times$ Ponderosa) and (June Pink $\times$ Ponderosa) $\times$ Ponderosa, have produced deep, fasciated fruits exclusively, according to expectation.

3. CROSSES in which the F_1 falls into Group 8 of Table III, namely, those in which the segregation is 3 shallow, non-fasciated : 1 shallow, fasciated (Cross VIII).

VIII. Bolgiano, *aabbffEE* $\times$ Dwarf Stone, *aabbFFEE*

F_1 , *aabbFfEE*

The parents, together with the F_1 and F_2 plants of this series

should all produce shallow fruits. Among 110 plants of the Bolgiano parent, 99 plants of the Dwarf Stone parent, 4 plants of the F_1 and 87 plants of the F_2 , no deep fruits have been found. Segregation in F_2 , independent of factors for depth, depends entirely upon the behavior of the F factor in the presence of the E factor, and is thus 3 non-fasciated: 1 fasciated. The segregation is 58:29, a ratio of 2.67:1.33. The deviation is 2.66 times the probable error and of little significance. (See Table V).

4. CROSSES in which the F_1 falls into Group 9 of Table III, namely, those in which the F_2 segregation is 9 deep, non-fasciated: 7 deep, fasciated (Cross IX).

IX. Ponderosa, $AABBf_{ee} \times$ Early Detroit, $AABBFFEE$
 F_1 , $AABBFfEe$

The cross Ponderosa $\times$ Early Detroit offers the first example of a 9:7 ratio resulting from the interaction of the two factors F and E to inhibit fasciation completely.

Ponderosa plants all produce much fasciated fruits; Early Detroit and the F_1 cross, non-fasciated fruits. The parents, as well as the F_1 and F_2 plants are all homozygous for the A and B factors, so that all fruits throughout the series are deep. In F_2 the segregation should be in the ratio 9 deep, non-fasciated: 7 deep, fasciated. A total of 183 plants of this generation was well classified during the summers of 1920 and 1921, 112 of which produced deep fruits with no suggestion of fasciation while 71 produced fruits fasciated in varying degrees. The observed ratio is 9.79:6.21. The deviation is 2.00 times the probable error and probably insignificant. (See Table V).

No question may be raised as to the accuracy of the classification in the F_2 from this cross. Attention has been called to the difficulty of recording the types of fruit when a segregation involves the B factor or the F factor alone. No such difficulty is encountered when the A and B factors or the F and E factors are both present, or both absent in the F_2 .

5. CROSSES in which the F_1 falls into Group 10 of Table III, namely, those in which the F_2 segregation is 9 deep, fasciated: 7 shallow, fasciated (Cross X).

X. Bolgiano, *aabbffEE* × Ponderosa, *AABBffee*

F₁, *AaBbffEe*

The Bolgiano parent is less fasciated than Ponderosa because of the presence of *EE*. The F₁ generation comprising 120 plants produced fruits of the general character of Ponderosa in depth, but with less fasciation because of heterozygosis of the *E* factor.

The F₂ plants all produce fasciated fruits according to expectation. A segregation possible of record in the field on the basis of depth alone gives a close approximation to the 9:7 ratio expected from the F₁ formula, *AaBb*. Fruits from 129 plants were recorded as deep, fasciated, from 70 plants as shallow, fasciated, a ratio of 10.37: 5.63. The deviation from expectation is 3.62 times the probable error. Such a deviation might be considered a significant one were it not for the fact, mentioned in the discussion of the cross June Pink × Ponderosa, that it is difficult to classify fasciated fruits as to depth. Further mention of the results of measuring many fruits in this series will be made in another paper. It is really remarkable, in view of the difficulty of classification, that such a close approximation to theory was obtained as that recorded.

6. CROSSES in which the F₁ falls into Group 14 of Table III, namely, those in which the segregation in F₂ follows the ratio 27 deep, non-fasciated: 21 deep, fasciated: 9 shallow, non-fasciated: 7 shallow, fasciated (Cross XI).

XI. Early Detroit, *AABBFFEE* × June Pink, *aaBBffee*

F₁, *AaBBFfEe*

Early Detroit, 125 plants, produced deep, non-fasciated fruits; June Pink, shallow, much fasciated fruits. All fruits on 21 F₁ plants were deep, non-fasciated.

In the F₂ cultures no attempt was made to distinguish between deep and shallow fruits. Certain plants producing deep, fasciated fruits, the Ponderosa type, were observed. The record shows that 63 plants produced non-fasciated fruits and 69 produced fasciated fruits. The ratio 27: 21: 9: 7 resolves itself into a ratio of 9 non-fasciated: 7 fasciated, if depth of fruit is disre-

garded. The observed ratio is 7.64 to 8.36. The deviation is 2.93 times the probable error.

The F_2 segregation in this cross is very striking. No easier task presents itself in the tomato garden than that of recording fasciated and non-fasciated fruits by direct observation. Further investigation may add numbers of plants to the record, but the present ratio furnishes sufficient proof for the necessity of assuming complementary factors for fasciation in these cultures.

7. CROSSES in which the F_1 falls into Group 15 of Table III, namely, those in which the F_2 segregation is 27 deep, non-fasciated: 21 shallow, non-fasciated: 9 deep, fasciated: 7 shallow, fasciated (Crosses XII, XIII).

XII. Bolgiano, *aabbffEE* $\times$ Early Detroit, *AABBFFEE*

F_1 , *AaBbFfEE*

The parent characters have been discussed (pp. 360-361). The F_1 plants, 45 in number, produced typical Early Detroit fruits, deep and with no fasciation.

No attempt was made to classify the non-fasciated fruits as to depth in the F_2 cultures. Considering fasciation alone the 27:21:9:7 ratio, above, becomes the ratio 48:16, or 3 non-fasciated:1 fasciated. In the F_2 , 61 plants produced non-fasciated fruits and 34 plants fasciated fruits, a ratio of 2.57:1.43. It is evident that such a classification should produce the concordant results reported for this cross. The deviation is 3.60 times the error. (See Table V.)

An attempt was made to classify as to depth of fruit the plants which produced fasciated fruits. This classification, as mentioned before, is difficult. The result, however, was not unsatisfactory. With the non-fasciated fruits unclassified and the fasciated fruits classified as to depth the foregoing ratio becomes 48 deep, non-fasciated + shallow, non-fasciated: 9 deep, fasciated: 7 shallow, fasciated. The observed frequencies were 61:18:16, a ratio of 41.10:12.13:10.78. The goodness of fit of this ratio is shown in Table V. By the χ^2 method, $\chi^2 = 4.193$ and P is .1250578. The differences shown in Table V are not of

great significance when the numbers of individuals and the difficulties in classification are considered.

XIII. John Baer, *AABBFFee* × Dwarf Stone, *aabbFFEE*

F₁, *AaBbFFEe*

The John Baer parent produces deep, somewhat fasciated fruits; the Dwarf Stone parent, shallow, non-fasciated fruits. In F₁, 45 plants produced deep, non-fasciated fruits.

In this case the classification of the fruits as to fasciation in F₂ is complicated by the presence of Dwarf plants upon which fruits fasciated to a marked degree seem never to appear. The plants were consequently classified as to depth of fruit alone. The ratio 27: 21: 9: 7 becomes on this basis the ratio 9 deep, fasciated + deep, non-fasciated: 7 shallow, fasciated + shallow, non-fasciated. The observed frequencies were 72: 66, a ratio of 8. 35: 7.65. The deviation is 2.12 times the error and insignificant. (See Table V.)

8. CROSSES in which the F₁ falls into Group 16 of Table III, namely, those in which the F₂ segregation is 81 deep, non-fasciated: 63 shallow, non-fasciated: 63 deep, fasciated: 49 shallow, fasciated (Crosses XIV to XVII).

XIV. Early Detroit, *AABBFFEE* × Dwarf Champion, *aabbfee*

F₁, *AaBbFfEe*

The cross involves two parents homozygous for all factors. The F₁, 25 plants, produced deep, non-fasciated fruits. No F₂ cultures were grown.

XV. Bolgiano, *aabbffEE* × John Baer, *AABBFFee*

F₁, *AaBbFfEe*

The parents have been discussed above (pp. 360-361). The F₁ plants, 81 in number, produced small, deep, non-fasciated fruits. It is unfortunate that time did not permit a large series of fruit measurements in this generation. An opportunity is here presented to study quantitatively a pedigree in which the

A and *B*, and the *F* and *E* factors are all in the heterozygous condition. The fruits were small as indicated above, but just how much the actual size is affected by such a combination of factors is unknown.

The F_2 plants were not classified as to depth. A sharp segregation was observed between the plants producing non-fasciated and those producing fasciated fruits. The record shows 96 of the former and 52 of the latter plants, a ratio of 10.49 to 5.51. (See Table V). As to fasciation alone the ratio 81:63:63:49 becomes 144:112 or 9 non-fasciated:7 fasciated. The deviation is 3.39 times the error.

XVI. Ponderosa, *AABBffee* $\times$ Dwarf Stone, *aabbFFEE*

F_1 , *AaBbFfEe*

The F_1 plants, 27 in number, produced, as in the preceding crosses, deep, non-fasciated fruits, smaller than the typical Ponderosa fruits.

In the F_2 the segregation was similar to that of the preceding cross (Bolgiano $\times$ Dwarf Stone). Plants with non-fasciated fruits numbered 43, those with fasciated fruits 30, a ratio of 9.43:6.58. The deviation from the expected 9:7 ratio, is 0.68 times the error and insignificant. A further classification of the F_2 plants with fasciated fruits shows 22 with deep fruits, i.e., of the Ponderosa type and 8 with shallow fruits. The ratio 81:63:63:49 becomes 144:63:49 on this basis. The close agreement of theory and observation is shown in Table V. By the χ^2 method, $\chi^2 = 3.081$ and $P = .2160186$.

XVII. Imperial, *AABBFFee* $\times$ Bolgiano, *aabbffEE*

F_1 , *AaBbFfEe*

Considerable quantitative data upon fruits from all generations of this cross are to be published in another paper.

Fifty F_1 plants produced typical, deep, non-fasciated fruits.

The segregation in F_2 and the close agreement of observation and theory are shown in Table V. The χ^2 test for goodness of fit gives for χ^2 the value .672, for P the value .866441. The fit is much better than would be expected from the classification of

98 plants. This cross is especially important since the whole hypothesis of complementary factors for depth and fasciation of tomato fruits was suggested by the segregation of the F_2 (Imperial $\times$ Bolgiano) into four types of fruit, one a typical Ponderosa, the second a typical Bolgiano, the third a typical large Globe type and the fourth a tiny Globe fruit which had not yet been observed by the writer. The first is deep, fasciated; the second, shallow, fasciated; the third, deep, non-fasciated and the fourth shallow, non-fasciated.

9. CROSSES in which the F_1 falls into several groups (Table III) because of the heterozygosis of one of the parents. The F_2 segregation depends upon the genotypic constitution of the self-pollinated F_1 individual (Crosses XVIII-XXI).

At this point the consideration of crosses which are of especial importance in establishing the suggested hypothesis ceases. The following crosses illustrate the employment of the hypothesis in the analysis of varieties of unknown constitution. The variety Discovery, as has been mentioned earlier in the paper, was for a long time a most puzzling one. Seed obtained by self-pollination produced plants bearing a motley array of fruit types. Mr. Starr recently informed the writer that he had tried unsuccessfully to "fix" the type. Crosses were made between two plants of Discovery and plants representing five varieties, the genotypic constitutions of which are now known. Both plants, D-1 and D-2, proved to be heterozygous for all factors for depth and fasciation.

XVIII. Discovery, $AaBbFfEe \times$ Ponderosa, $AABBffee$

F_1

Deep, fasciated (12)

$AABBFfee$ $AABBffee$
 $AABbffeE$ $AABbffee$
 $AABbffeE$ $AaBBffee$
 $AaBBffeE$ $AaBbffeE$
 $AABbFfee$ $AaBbFfee$
 $AaBBFfee$ $AaBbffee$

Deep, non-fasciated (4)

$AABBFfEe$
 $AABbFfEe$
 $AaBBFfEe$
 $AaBbFfEe$

F_1 ratio = 3 deep, fasciated: 1 deep, non-fasciated.

All F_1 individuals produce deep fruits. The ratio should be then 3 fasciated:1 non-fasciated. Twenty-seven plants were grown, 17 of which bore fasciated fruits and 10 non-fasciated fruits. The ratio is 2.52:1.48 and the deviation 2.14 times the error.

A paradox of considerable interest obtains in this cross. In F_1 there is a ratio of 3 fasciated:1 non-fasciated; in the F_2 a ratio of 9 non-fasciated:7 fasciated. The former ratio is, of course, never possible in F_2 but the illustration shows how very puzzling are some of the phenomena observed in crosses with heterozygous strains.

A single plant of the F_1 which produced deep, non-fasciated fruits was selected for self-pollination. That the genotypic constitution of this plant was $AABBFfEe$ is certain. No plants were found in the F_2 which produced shallow fruits as would have been expected had the genotypic formula of the F_1 individual been $AABbFfEe$, $AaBBFfEe$ or $AaBbFfEe$. The observed F_2 ratio was 67 deep, non-fasciated:32 deep, fasciated, or 10.83:5.17. The deviation from the expected 9:7 ratio is 3.40 times the probable error.

XIX. Discovery, $AaBbFfEe \times$ Bolgiano, $aabbffEE$

F_1

Deep, non-fasciated (2)

$AaBbFfEE$

$AaBbFfEe$

Deep, fasciated (2)

$AaBbffEE$

$AaBbffEe$

Shallow, non-fasciated (6)

$AabbFfEE$ $aaBbFfEe$

$AabbFfEe$ $aabbFfEE$

$aaBbFfEE$ $aabbFfEe$

Shallow, fasciated (6)

$AabbffEE$ $aaBbffEe$

$AabbffEe$ $aabbffEE$

$aaBbffEE$ $aabbffEe$

F_1 plants were classified as to fasciation but not as to depth of fruit. Of 13 plants 5 bore non-fasciated, and 8 bore fasciated fruits. The ratio is .77:1.23, a deviation of 0.23 from the theoretical 1:1 ratio. The frequencies are too few for any theoretical reasoning, but it is significant that among 13 plants the ob-

served ratio should agree so closely with the theoretical expectation. The fruits of the F_1 individual selected for pollination were fasciated. The comparative depth of these fruits is not known since the plant was grown in the greenhouse and but two fruits allowed to develop.

The segregation in F_2 points to the conclusion that the genotypic constitution of the F_1 plant was *AaBbffEE*. The segregation expected from such an individual is 9 deep, fasciated: 7 shallow, fasciated. Of the F_2 plants, 44 produced deep, fasciated fruits, 53 bearing shallow, fasciated fruits. The deviation is 3.20 times the error. This deviation is too large, but attention is again called to the fact that it is always difficult to classify as to depth among fasciated fruits without actually measuring the vertical diameters.

It is difficult to resist the temptation to digress for a moment at this point, in order to comment upon the reaction of certain commercial breeders to the observation of situations such as obtain in this particular cross. The variety Discovery, if indeed it may be termed a variety, is supposed to bear deep, non-fasciated fruits. Such fruits are of the Globe type and very desirable. A plant is selected by the breeder which bears the fruit desired. Among the progeny of this plant are plants producing deep and shallow fruits, fasciated and non-fasciated fruits. The selection process is carried further with the same result year after year and the conclusion is reached that it is impossible to "fix" the type. Discovery is now crossed with Bolgiano, an early, shallow-fruited variety. The F_1 includes large and small Globes, fruits like those of the parent Bolgiano and a new type, the deep, fasciated fruits of Ponderosa. Thus are new varieties "produced." The list of named varieties of tomatoes is a long one.

A single glance at the genotypes in F_1 , Discovery $\times$ Bolgiano, in which the Discovery individual was heterozygous for all factors will reveal the fact that none of the F_1 plants will breed true for the Globe type, nor Ponderosa type, but that all of the Bolgiano-like plants will forever breed true for the shallow, fasciated characters.

XX. Discovery, *AaBbFfEe* × Earliana, *aabbffEE*F₁, as in the cross Discovery × Bolgiano.

The present cross is identical in every way with the cross Discovery × Bolgiano and needs no discussion except as to the F₂ segregation. In the F₁, 15 plants produced non-fasciated fruits, 14 plants fasciated fruits, a ratio of 1.03: .97, which deviates from the expected 1: 1 ratio by only .03. This deviation is 0.27 times the error and is insignificant. (See Table V).

In the F₂ a new situation arises. Instead of the 9 deep, fasciated: 7 shallow, fasciated, of the cross Discovery × Bolgiano, the ratio is 3 shallow, non-fasciated: 1 shallow, fasciated. The observed frequencies are 63: 34, a ratio of 2.60: 1.40. Only an F₁ individual of the genotypic constitution *aabbFfEE* could have produced such a ratio. (See Table III.)

XXI. Discovery, *AaBbFfEe* × June Pink, *aaBBffee*F₁

Deep, non-fasciated (2)

*AaBBFfEe**AaBbFfEe*

Deep, fasciated (6)

*AaBBffee AaBbffEe**AaBbffEe AaBbFfee**AaBBffee AaBbffee*

Shallow, non-fasciated (2)

*aaBBFfEe**aaBbFfEe*

Shallow, fasciated (6)

*aaBBffEe aaBbFfee**aaBbFfee aaBBffee**aaBbffEe aaBbffee*

Again, the F₁ segregation was recorded as to fasciation alone. The formulae above indicate an expected ratio of 1 non-fasciated: 3 fasciated. The observed frequencies are 15: 35, a ratio of 1.20: 2.80. The deviation is 2.21 times the error and is insignificant.

In F₂ with the same classification a ratio of 9 non-fasciated: 7 fasciated was approached. The frequencies are 46: 51, a ratio of 7.59: 8.41. The deviation is 2.60 times the error.

The classification made in this pedigree renders it possible that a few of the plants recorded as bearing non-fasciated fruits may have been included among those recorded as fasciated. The

ratio is sufficiently near 9:7, however, to warrant the assumption of *AaBBFfEe* as the genotypic constitution of the F_1 self-fertilized individual. Fruits from this plant were deep, non-fasciated. Record is made of the fact that the depth of fruit varies from plant to plant, although no accurate classification of plants as to depth of fruit was attempted. An F_1 individual of the formula *aaBBFfEe* or *aaBbFfEe* would have produced plants segregating 9:7 for fasciation, but with shallow fruits.

APPLICATION OF HYPOTHESIS TO DATA OF PREVIOUS WRITERS

Price and Drinkard (1908, p. 30) give the ratio obtained in the F_2 generations from a cross between a variety with roundish-conic fruits and one with roundish-compressed fruits. The ratio is 35 conic:13 compressed or 2.92:0.08, a very close fit to a 3:1 ratio. The difference (0.08) is but 0.49 times the probable error (0.17) and is insignificant.

This is the only record which has come to the writer's attention of a segregation between the characters discussed in the present paper. The explanation is quite simple. It is only necessary to assume that the two individuals crossed by Price and Drinkard were of the formulae *AABBFFEE* (deep, non-fasciated) and *aaBBFFEE* (shallow, non-fasciated). The F_1 genotype would thus be *AaBBFFEE* (deep, non-fasciated). The F_2 generation would split into 3 deep, non-fasciated (roundish, conic):1 shallow, non-fasciated (roundish, compressed). The authors do not mention fasciation. With all of the facts in hand the genotypes might prove to be different from those suggested. It is not necessary, however, to go beyond the suggested hypothesis for an explanation of the behavior observed by Price and Drinkard in the foregoing cross.

SUMMARY OF 9:7 RATIOS

The proof of a complementary factor hypothesis must be sought in the familiar 9:7 Mendelian ratio. Collected in Table VI are all of the 9:7 ratios which have been observed in these crosses. Such a segregation for depth is from the genotype

AaBb and for fasciation from the genotype *FfEe*. These genotypes are the same, of course, regardless of their origin. The summation of all segregations for depth and of all segregations for fasciation eliminates the errors of the small sample. The result is a ratio of 9.23:6:77 for depth among 603 individuals and a ratio of 9.30:6.70 for fasciation among 854 individuals. In each instance the deviation is approximately equal to the error. In the light of such results the writer hesitates not at all in suggesting a complementary factor hypothesis for both depth and fasciation.

SUMMARY AND CONCLUSIONS

1. Crosses have been made among ten varieties of the garden tomato, eight of which produce different types of fruit.
2. Each fruit type is produced as a result of a particular combination of depth and fasciation factors.
3. The complementary factors *A* and *B* determine the depth of the fruits. Genotypes having *A* in the presence of *B* produce deep fruits. Those having *A* or *B* in a homozygous condition produce fruits, but slightly deeper than the shallow fruits produced by genotypes with the factors *a* and *b*.
4. The complementary factors *F* and *E* inhibit fasciation. Genotypes having *F* in the presence of *E* produce non-fasciated fruits. Slightly fasciated fruits which may be considered to be teratological are produced in rare instances by such genotypes. Genotypes having either *F* or *E* (but not both) in the homozygous condition produce fruits in which fasciation is inhibited only to a slight degree. The normal allelomorphs (*f* and *e*) of the factors *F* and *E* determine the production of fasciated fruits.
5. A critical examination of the data upon twenty-one crosses made by the writer and one cross reported by Price and Drinkard, in which the F_2 behavior as to fruit type has been recorded, fails to bring to light a single instance in which the depth-fasciation hypothesis is incapable of accounting for the observed phenomena.
6. It has been possible to explain many curious phenomena observed in the tomato cultures by the use of the working hy-

pothesis suggested. Such phenomena as the appearance of a Ponderosa type among the F_2 progeny of a cross between two varieties (Imperial and Bolgiano) which bear smaller fruits, the appearance of deep, non-fasciated (Globe type) fruits in the F_2 generation of crosses between varieties which bear fasciated fruits (Imperial $\times$ Bolgiano), the appearance of tiny non-fasciated fruits among the F_2 plants from a cross between two varieties (Dwarf Stone and Bolgiano) which bear larger fruits, all of these require the assumption of complementary factors for their explanation.

7. The factors here identified have explained certain phenomena which otherwise must have been explained by a hybrid vigor hypothesis. Certain crosses produce F_1 plants with larger fruits than those of the parents (e.g., Earliana $\times$ June Pink), but in many more crosses (e.g., June Pink $\times$ Ponderosa) the F_1 fruits are smaller. Quantitative data to prove these points are to be presented in another paper, but let it be noted here that these results are to be expected from the depth-fasciation hypothesis and need no further explanation.

8. Measurements of the depth, width, weight and stem depression of many fruits in these cultures have been made. In each of the six crosses which have been investigated in this manner the quantitative data confirm the present hypothesis. These data will be published soon.

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TABLE I
MENDELIAN CHARACTERS IN THE GARDEN TOMATO
(from Jones, *American Naturalist*, LI. 618)

	Dominant	Recessive
Fruit shape	1 Spherical (non-constricted)	Pyriform (constricted)
Fruit shape	2 Roundish conic	Roundish compressed
Loculation of ovary	3 Bilocular	Plurilocular
Endocarp color	4 Red	Yellow
Epicarp color	5 Yellow	Colorless
Fruit surface	6 Smooth	Pubescent
Vine habit and leaf surface	7 {Standard Smooth	{Dwarf Rugose
Leaf margin	8 Serrate (normal or fine leaf)	Entire ("potato" or coarse leaf)
Leaf type	9 <i>Pimpinellifolium</i> type	<i>Esculentum</i> type
Foliage color	10 Green	Yellow
Inflorescence type	11 Simple	Compound

TABLE II

PEDIGREE LIST OF ALL PARENTS AND CROSSES WITH THE NUMBER OF MATURE PLANTS RECORDED AMONG THE PROGENY

Varieties are designated in the pedigrees as follows: B, Bolgiano; JP, June Pink; P, Ponderosa; E, Earliana; I, Imperial; JB, John Baer; D, Discovery; ED, Early Detroit; DC, Dwarf Champion; DS, Dwarf Stone.

PARENT STRAINS

Pedigree	Progeny	Pedigree	Progeny	Pedigree	Progeny
B	11	E-3	11	ED	22
B-6	48	E-1	20	ED-2	12
B-7	26	E-3-4-2	50	ED-2-7 op-1	91
B-9	25	E-1-16-2	49		
				DC	20
JP-1	19	I	18	DC-1	25
JP-1-10-2	99	I-5	75	DC-1-1	25
				DC-15-1	25
P-1	9	JB	19		
P-3	19	JB-1-1	98	DS	19
P-3-1	50			DS-5	80
P-3-1-2	50	D	23		
		D-1-1	71		

TABLE II — *Continued*

CROSSES

Cross No.	Generation	No. of Progeny	Pedigree
I	F ₁	50	JP-1-10 × B-6
	F ₂	51	(B-6 × JP-1-1)-1
		50	(JP-1-10 × B-6)-1
II	F ₁	50	B-7 × E-3-4
		50	E-3-4 × B-7
	F ₂	75	(B-7 × E-3-4)-1
		74	(E-3-4 × B-7)-1
III	F ₁	41	E-1 × JP-1
		13	JP-2 × E-1
	F ₂	100	(E-1 × JP-1)-26
		31	(JP-2 × E-1)-1
		100	(JP-2 × E-1)-10
IV	F ₁	38	B-6 × DC-15
		8	DC-15 × B-6
	F ₂	76	(B-6 × DC-15)-1
		75	(DC-15 × B-6)-1
V	F ₁	55	JP-1-10 × DC-1
		9	DC-1 × JP-1-10
	F ₂	74	(JP-1-10 × DC-1)-1
		74	(DC-1 × JP-1-10)-1
		124	(DC-1 × JP-1-10)-1 × JP-1-10-2
		124	DC-1-1 × (DC-1 × JP-1-10)-2
VI	F ₁	8	JB-1 × P-3-1
	F ₂	50	(JB-1 × P-3-1)-1
		49	(JB-1 × P-3-1)-2
		100	P-3-1-1 × (JB-1 × P-3-1)-1
		10	(JB-1 × P-3-1)-2 × P-3-1-1
		97	JB-1-1 × (JB-1 × P-3-1)-1
		89	(JB-1 × P-3-1)-1 × JB-1-2
VII	F ₁	71	JP-1 × P-1
		24	P-1 × JP-1
	F ₂	63	(JP × P)-2
		18	(JP × P)-6
		51	(JP-1 × P-1)-18
	F ₃	51	(JP × P)-6-15
		52	(JP × P)-2-9
		20	(JP × P)-2-11
		35	JP-1-10 × (JP-1 × P-1)-18
		58	(JP-1 × P-1)-18 × JP-1-10
		51	JP-3 × (JP × P)-10
		45	(JP × P)-10 × JP-3
		151	JP-1 × (JP × P)-7

TABLE II—*Concluded*

CROSSES

Cross No.	Generation	No. of Progeny	Pedigree
VIII	F ₁	96	(JP × P)-7 × JP-1
		74	P-3 × (JP × P)-6
		55	(JP-1 × P-1)-18 × P-1-2
IX	F ₂	2	DS-5 × B-6
		87	(DS-5 × B-6)-2
		3	P × ED (Greenhouse)
X	F ₁	90	(P × ED)-1
		74	(P × ED)-2
		19	(ED × P)-1 × (ED × P)-2
XI	F ₂	45	B-6 × P-3-1
		75	P-3-1 × B-6
		50	(B-6 × P-3-1)-1
XII	F ₁	51	(B-6 × P-3-1)-2
		98	(P-3-1 × B-6)-1
		53	ED-2 × JP-1
XIII	F ₂	98	(ED-2 × JP-1)-3
		34	(ED-2 × JP-1)-16
		45	ED-2-7 × B-5
XIV	F ₁	95	(ED-2-7 × B-5)-1
		17	DS-3 × JB-13
		45	JB-13 × DS-3
XV	F ₂	63	(DS-3 × JB-13)-1
		75	(JB-13 × DS-3)-1
		25	DC-1 × ED-2-12
XVI	F ₁	75	B-6 × JB-13
		6	JB-13 × B-6
		75	(B-6 × JB-13)-1
XVII	F ₂	73	(JB-13 × B-6)-2
		27	P-3-1 × DS-3
		73	(P-3-1 × DS-3)-2
XVIII	F ₁	50	I-5 × B-7
		98	(I-5 × B-7)-2
		27	P-3-1 × D-1
XIX	F ₂	99	(P-3-1 × D-1)-1
		3	B-6 × D-1
		10	D-1 × B-6
XX	F ₁	97	(D-1 × B-6)-1
		29	D-1 × E-3-8
		97	(D-1 × E-3-8)-1
XXI	F ₂	50	JP-1-10 × D-2
		99	(JP-1-10 × D-2)-1

TABLE III

POSSIBLE GENOTYPES AND THE PHENOTYPIC CONSTITUTION
OF THEIR PROGENIES

A in the presence of B = Deep Fruit; F in the presence of
E = Non-fasciated Fruit.

GROUP	GENOTYPIC FORMULAE			CHARACTER OF PROGENY
1	<i>AABBBFFEE</i>			All deep, non-fasciated
2	<i>AABBBFfee</i>	<i>AABBffEE</i>	<i>AABBffee</i>	All deep, fasciated
	<i>AABBFfee</i>	<i>AABBffEe</i>		
3	<i>AAbbFFEE</i>	<i>aaBBFFEE</i>	<i>aabbFFEE</i>	All shallow, non-fasciated
	<i>AabbFFEE</i>	<i>aaBbFFEE</i>		
4	<i>Aabbffee</i>	<i>aaBBffee</i>	<i>aabbFFee</i>	All shallow, fasciated
	<i>aabbffEE</i>	<i>AabbFFee</i>	<i>AAbbffEE</i>	
	<i>aaBBFFee</i>	<i>aaBBffEE</i>	<i>aabbffee</i>	
	<i>Aabbffee</i>	<i>aaBbffee</i>	<i>aabbFfee</i>	
	<i>aabbffEe</i>	<i>AAbbFfee</i>	<i>AAbbffEe</i>	
	<i>aaBBFfee</i>	<i>aaBBffEe</i>	<i>AabbFFee</i>	
	<i>aaBbFFee</i>	<i>AabbffEE</i>	<i>aaBbffEE</i>	
	<i>AabbFfee</i>	<i>AabbffEe</i>	<i>aaBbFfee</i>	
	<i>aaBbffEe</i>			
5	<i>AABbFFee</i>	<i>AABbffEE</i>	<i>AAAbffee</i>	3 deep, fasc.: 1 shallow, fasc.
	<i>AaBBFFee</i>	<i>AaBBffEE</i>	<i>AaBBffee</i>	
	<i>AABbFfee</i>	<i>AABbffEe</i>	<i>AaBBffEe</i>	
	<i>AaBBFfee</i>			
6	<i>AABBBFFee</i>	<i>AABBBFFEE</i>		3 deep, non-f.: 1 deep, fasc.
7	<i>AABbFFEE</i>	<i>AaBBFFEE</i>		3 deep, non-f.: 1 shallow, non-f.
8	<i>AAbbFFEe</i>	<i>AAbbFfEE</i>	<i>aaBBFFEe</i>	3 shallow, non-f.: 1 shallow, fasc.
	<i>aaBBFFEE</i>	<i>aabbFFEe</i>	<i>aabbFfEE</i>	
	<i>AabbFFEe</i>	<i>AabbFfEE</i>	<i>aaBbFFEe</i>	
	<i>aaBbFfEE</i>			
9	<i>AABBFfEe</i>			9 deep, non-f.: 7 deep, fasc.
10	<i>AaBbFFee</i>	<i>AaBbffEE</i>	<i>AaBbffee</i>	9 deep, fasc.: 7 shallow, fasc.
	<i>AaBbFfee</i>	<i>AaBbffEe</i>		
11	<i>AAbbFfEe</i>	<i>aaBBFfEe</i>	<i>aabbFfEe</i>	9 shallow, non-f.: 7 shallow, fasc.
	<i>AabbFfEe</i>	<i>aaBbFfEe</i>		
12	<i>AaBbFFEE</i>			9 deep, non-f.: 7 shallow, non-f.
13	<i>AABbFFEe</i>	<i>AABbFfEE</i>	<i>AaBBFFEe</i>	9 deep, non-f.: 3 deep, fasc.: 3 shallow, non-f.: 1 shallow, fasc.
	<i>AaBBFfEE</i>			
14	<i>AABbFfEe</i>	<i>AaBBFfEe</i>		27 deep, non-f.: 21 deep, fasc.: 9 shallow, non-f.: 7 shallow, fasc.
15	<i>AaBbFFEe</i>	<i>AaBbFfEE</i>		27 deep, non-f.: 21 shallow, non-f.: 9 deep, fasc.: 7 shallow, fasc.
16	<i>AaBbFfEe</i>			81 deep, non-f.: 63 shallow, non-f.: 63 deep, fasc.: 49 shallow, fasc.

TABLE IV
 GENOTYPES INVESTIGATED WITH THE PHENOTYPIC CONSTITUTION OF THEIR PROGENIES
 D = Deep; S = Shallow; F = Fasciated; N = Non-fasciated

Group	Genotypic Formula	Pheno-type	No. Pl.	Ped.	Gen.	Number of Plants in Progeny							Total		
						D-F	D-N	S-F	S-N	D	S	F		N	
1	AABBBFFEE	D-N	125	ED	P ₁										
2	AABBBFFee	D-F	117	JB	P ₁										
	AABBBFFee	D-F	93	I	P ₁										
	AABBBfee	D-F	128	P	P ₁										
3	AABBBFfee	D-F	8	JB × P	F ₁										
4	aabbFFEE	S-N	99	DS	P ₁					99				99	99
	aaBBjfee	S-F	118	JP	P ₁										
	aabbjfee	S-F	130	E	P ₁										
	aabbjfee	S-F	110	B	P ₁										
	aabbjfee	S-F	100	B × E	F ₁										
	aabbjfee	S-F	95	DC	P ₁						149		149		149
	aaBbjfEe	S-F	50	B × JP	F ₁							101	101		101
	aaBbjfEe	S-F	54	E × JP	F ₁							231	231		231
	aabbjfee	S-F	46	B × DC	F ₁							151	151		151
	aaBbjfee	S-F	64	JP × DC	F ₁							148	148		148
5	AaBBjfee	D-F	95	JP × P	F ₁	26				26		6	32		32
				JP × P	F ₁								132		132
8	aabbFjEE	S-N	2	B × DS	F ₁				58	87		29	58		87

TABLE IV—Continued

9	<i>aabbFfEe</i>	S-N	1	D × E	F ₁	71	63	34	63	34	63	97
	<i>AABBFfEe</i>	D-N	3	P × ED	F ₁	112	183		183	71	112	183
	<i>AABBFfEe</i>	D-N	1	P × D	F ₁	32	99		99	32	67	99
	<i>AaBbfEe</i>	D-F	120	B × P	F ₁	129	129	70	129	199		199
10	<i>AaBbfEE</i>	D-F	1	D × B	F ₁	44	44	53	44	53	97	97
	<i>AaBBFfEe</i>	D-N	53	ED × JP	F ₁					69	63	132
15	<i>AaBBFfEe</i>	D-N	1	D × JP	F ₁					51	46	97
	<i>AaBbfEE</i>	D-N	45	B × ED	F ₁	18		16		34	61	95
	<i>AaBbFfEe</i>	D-N	62	JB × DS	F ₁				72	66		138
	<i>AaBbFfEe</i>	D-N	1	D	F ₁	19	25		44	27	25	71
16	<i>AaBbfEe</i>	D-N	81	B × JB	F ₁	22		8	22	52	96	148
	<i>AaBbFfEe</i>	D-N	27	P × DS	F ₁	25		17	59	30	43	73
	<i>AaBbFfEe</i>	D-N	50	I × B	F ₁					8	39	98
	<i>AaBbFfEe</i>	D-N									42	56

CROSSES BETWEEN HOMOZYGOTES AND HETEROZYGOTES

Group	Heterozygote	Homozygote	Pedigree	D-F	D-N	S-F	S-N	D	S	F	N
2	<i>AABBFfEe</i> <i>AABBFfEe</i>	<i>AABBFfEe</i> <i>AABBFfEe</i>	(JB × P) × P (JB × P) × JB	110 186			110 186		110 186		110 186
4	<i>aABbfEe</i> <i>aABbfEe</i>	<i>aaBBfEe</i> <i>aaBBfEe</i>	(DC × JP) × JP (DC × JP) × DC			124 124	124 124	124 124	124 124		124 124
5	<i>AaBBfEe</i> <i>AaBBfEe</i>	<i>AaBBfEe</i> <i>AaBBfEe</i>	(JP × P) × JP (JP × P) × P	142 129		123	142 129	123	265 129		265 129
16	<i>AaBbFfEe</i> <i>AaBbFfEe</i>	<i>aaBBfEe</i> <i>aaBBfEe</i>	D × B D × E D × P D × JP	10	15 17	14	15 27	14	8 14 10 35	5 15 17 15	13 29 27 50

TABLE V

TESTS FOR GOODNESS OF FIT OF MENDELIAN RATIOS FOR DEPTH AND
FASCIATION OF FRUIT OBSERVED IN THE F_1 , F_2 GENERATIONS
AND IN THE BACK-CROSSES

Group in Text	Cross and Generation	Observed Frequency	Observed Ratio	Theoretical Ratio	Deviation	Probable Error	Dev./P. E.
VI	F_2 -P $\times$ JB	75 Less Fasc.	3.03	3			
		24 More Fasc.	0.97	1	0.03	0.12	0.26
	P $\times$ (JB $\times$ P)	61 More Fasc.	1.11	1			
		49 Less Fasc.	0.89	1	0.11	0.06	1.70
VII	F_2 -JP $\times$ P	26 Deep Fasc.	3.25	3			
		6 Shallow Fasc.	0.75	1	0.25	0.65	0.38
	JP $\times$ (JP $\times$ P)	142 Deep Fasc.	1.07	1			
		123 Shallow Fasc.	0.93	1	0.07	0.04	1.74
VIII	F_2 -B $\times$ DS	58 Shallow Non-F.	2.67	3			
		29 Shallow Fasc.	1.33	1	0.33	0.13	2.66
IX	F_2 -P $\times$ ED	112 Deep Non-F.	9.79	9			
		71 Deep Fasc.	6.21	7	0.79	0.40	2.00
X	F_2 -B $\times$ P	129 Deep Fasc.	10.37	9			
		70 Shallow Fasc.	5.63	7	1.37	0.38	3.62
XI	F_2 -ED $\times$ JP	63 Non-F.	7.64	9			
		69 Fasc.	8.36	7	1.36	0.47	2.93
XII	F_2 -B $\times$ ED	61 Non-F.	2.57	3			
		34 Fasc.	1.43	1	0.43	0.12	3.60
		61 Non-F.	41.10	48	6.91	1.92	3.60
		18 Deep Fasc.	12.13	9	3.13	1.54	2.03
		16 Shallow Fasc.	10.78	7	3.78	1.38	2.73
		72 Deep	8.35	9			
XIII	F_2 -JB $\times$ DS	66 Shallow	7.65	7	0.65	0.31	2.12
		96 Non-F.	10.49	9			
XV	F_2 -B $\times$ JB	52 Fasc.	5.51	7	1.49	0.44	3.39
		43 Non-F.	9.43	9			
XVI	F_2 -P $\times$ DS	30 Fasc.	6.58	7	0.43	0.63	0.68
		43 Non-F.	150.80	144	6.80	10.03	0.68
		22 Deep Fasc.	77.15	63	14.15	8.70	1.63
		8 Shallow Fasc.	28.06	49	20.95	7.95	2.64
		34 Deep Non-F.	88.82	81	7.82	8.11	0.96
XVII	F_2 -I $\times$ B	22 Shallow Non-F.	57.47	63	5.53	7.51	0.74
		25 Deep Fasc.	65.31	63	2.31	7.51	0.31
		17 Shallow Fasc.	44.41	49	4.59	6.86	0.67
		17 Deep Non-F.	2.52	3			
XVIII	F_1 -D $\times$ P	10 Deep Fasc.	1.48	1	0.48	0.23	2.14
		67 Deep Non-F.	10.83	9			
	F_2 -D $\times$ P	32 Deep Fasc.	5.17	7	1.83	0.54	3.40

TABLE V — *Concluded*

Group in Text	Cross and Generation	Observed Frequency	Observed Ratio	Theoretical Ratio	Deviation	Probable Error	Dev./P.E.
XIX	F ₁ -D × B	5 Non-F. 8 Fasc.	0.77 1.23	1	0.23	0.19	1.24
	F ₂ -D × B	44 Deep Fasc. 53 Shallow Fasc.	7.26 8.74	9			
				7			
XX	F ₁ -D × E	15 Deep Non-F. 14 Shallow Fasc.	1.03 0.97	1	0.03	0.13	0.27
	F ₂ -D × E	63 Shallow Non-F. 34 Shallow Fasc.	2.60 1.40	3			
				1			
XXI	F ₁ -D × JP	35 Fasc. 15 Non-F.	2.80 1.20	3	0.20	0.17	2.21
	F ₂ -D × JP	46 Non-F. 51 Fasc.	7.59 8.41	9			
				7			

TABLE VI

SUMMARY OF 9:7 RATIOS FOR DEPTH AND FASCIATION

Cross No.	Cross	Number of Plants with		Number of Plants with	
		Deep Fruits	Shallow Fruits	Non-fasciated Fruits	Fasciated Fruits
IX	D × Self	44	27	25	19
	P × ED			112	71
X	B × P	129	70		
XI	ED × JP			63	69
XIII	DS × JB	72	66		
XV	B × JB			96	52
XVI	P × DS			43	30
XVII	I × B	59	39	56	42
XVIII	P × D			67	32
XIX	B × D	44	53		
XXI	JP × D			46	51

Total No. of Plants.....	348	:	255/603	508	366/874
Observed Ratio.....	9.23	:	6.77	9.30	: 6.70
Theoretical Ratio.....	9.00	:	7.00	9.00	: 7.00
Deviation.....	0.23			0.30	
Probable Error.....	0.22			0.18	
Dev./P. E.....	1.05			1.67	

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